심리학석사학위논문

Temporal Order Judgment of Monkey

원숭이의 시간 순서 판단 과제 수행 분석

2014년 2월

서울대학교 대학원
심 리 학 과
심 진 우

Temporal Order Judgment of Monkey

지도교수 이 춘 길

이 논문을 심리학석사 학위논문으로 제출함.

2014년 2월

서울대학교 대학원

심 리 학 과

심 진 우

심진우의 심리학석사 학위논문을 인준함.

2014년 2월

위 원 장 오 성 주

부위원장 이 상 훈

위 원 이 춘 길

Abstract

Jinwoo Sim

Department of Psychology

The Graduate School of

Seoul National University

The aim of this study was to develop a temporal order judgment (TOJ) task for monkeys and to investigate monkeys' performance. Two trained monkeys (*Macaca Fascicularis)* performed a two-alternative forced choice TOJ task in which the subject made a saccadic eye movement toward one of two Gabor stimuli. Two stimuli were presented in the left and right side of fixation with a temporal asynchrony of 0, 10, or 30ms. A few drops of fluid as reward was delivered when the subject made a saccadic eye movement to the earlier one of the two. For the asynchrony of zero, reward was delivered in randomly-chosen half of trials, regardless of the subject's choice. Analyses of behavioral data revealed following results. First, a significant difference in the mean reaction time between correct and incorrect trials was observed, but the pattern of difference across temporal asynchrony conditions was depended on subjects. Second, response bias and correct rate were correlated with each other, but the pattern and the strength of the relationship differed between two subjects. Third, strong correlation of biases was found

between conditions when stimuli were presented asynchronously (i.e. correct answer exists.) or presented simultaneously (i.e. correct answer doesn't exists.). Fourth, when targets were presented simultaneously, animal's choice was predictable with a logistic regression model, using reward history and previous choices as indicators. But the models differ between subjects. These results suggest that two monkeys used different strategies while performing the same TOJ task.

Keywords: Temporal order judgment, Reward history, Response bias, Reaction time distribution, Neural latency

Student Number: 2011-20125

Contents

Figures

Tables

1. Introduction

1.1. Decision Model and Accumulation of Evidence

We interact with our surroundings every moment and make decisions when necessary. Our perceptual systems are always ready for occurrence of new events and help us get prepared for appropriate responses. For example, when our visual system caught something fly towards us, we immediately try to dodge the object. For this simple dodging behavior at the moment, our visual system gathers information about the flying object's properties (e.g. direction, speed) and makes decisions about the objects identities so that our appropriate action can take place in proper way.

To explain this process of our visuomotor system, many decision models have been proposed (Becker, DeGroot, & Marschak, 1964; Carpenter, 1981; LaBerge, 1962, 1994; Link & Heath, 1975; Purcell, Schall, Logan, & Palmeri, 2012; Roger Ratcliff, 1978; Schall, Purcell, Heitz, Logan, & Palmeri, 2011; E. E. Smith, 1968; P. L. Smith & Vickers, 1988; Stone, 1960; Williams, 1995). Although they vary widely in details, most of them assume that when the amount of accumulated information exceeds a certain level of threshold, decision is made (Fig 1). When the outside event occurs and the visual system catches the event, the information about the event arrives at some accumulation stage. If the signal intensity from the event is strong enough or the signal persists after its appearance, the information keeps flowing into the accumulator unit

and the unit starts to accumulate the evidence it receives. When the level of accumulation reaches a certain threshold, the system makes a decision.

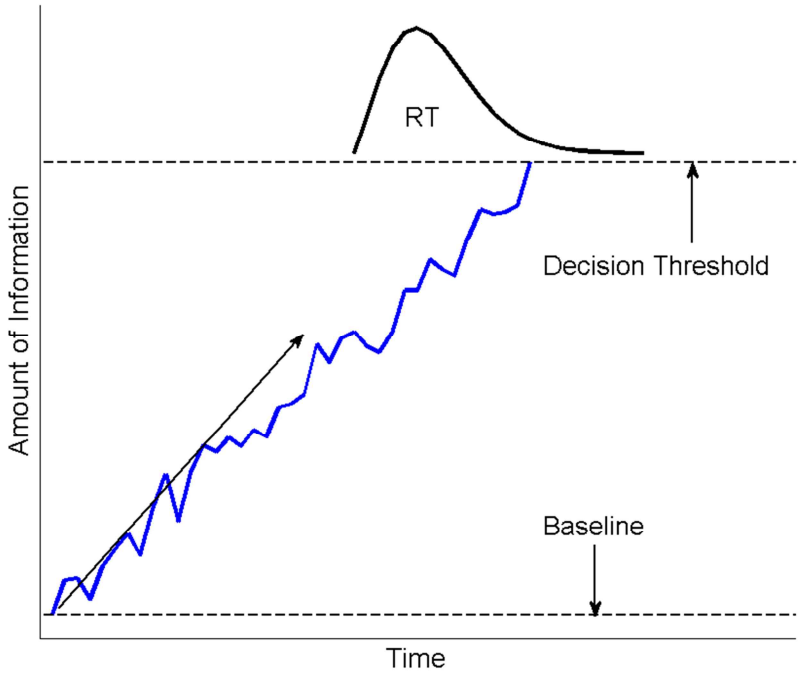

Figure 1. Illustration of accumulator model. Y axes represent the degree of accumulator unit's activity which represents the amount of accumulated information. Blue trace is the amount of information accumulated at any given time. Black dashed line below shows baseline activity of accumulator unit in the absence of information arrival, and another dashed line above represents the threshold level where the unit makes a decision. The positively skewed distribution shown above threshold level is a predicted reaction time distribution when the rate of accumulation follows a Gaussian distribution. In this model, latency of information arrival is not included in the process of decision making.

The rate of accumulation is determined by the intensity of the visual events. If intensity is high, the accumulation rate is high resulting in a short accumulation time to threshold. In some models (Purcell et al., 2012; R. Ratcliff, Hasegawa, Hasegawa, Smith, & Segraves, 2007; Story & Carpenter, 2009) that assume a competition between accumulation units, the rate determines not only reaction time but also the direction of decision. Therefore, the rate of accumulation plays a critical role in decision models.

This process of accumulation to threshold has been proposed in many psychological and neurological studies, emphasizing that the rate of accumulation is a critical factor of the process. However, there are other factors that also influence the accumulation rate, and thus reaction time and the direction of decision. For example, the start of accumulation that reflects the arrival latency of information at the accumulator is related to the time taken by the stages where the information went through before it arrives to the accumulator unit. Strictly, it is not a factor that can be dealt within the model of decision making. Rather, arrival latency is considered to be of pre-processing of the information before it became acceptable to the accumulator. Therefore, it has been ignored or set as a constant in most cases.

1.2. Latency of Neural Signal

The arrival latency have its own valuable information. One of the known encoding scheme used by the brain is ‘Timing Coding’ (Gerstner, Kreiter, Markram, & Herz, 1997; Thorpe, 1990), which is based on the temporal features of neural signals to

transfer information to other neurons. For example, a receiver neuron may decode the information by utilizing the arrival latency of the signal.

Timing coding scheme can also be found in the visual system. Lee, Kim, and Lee (2010) trained two macaque monkeys to perform a simple detection task while recording the activity of V1 neurons that encoded saccade target's (a circular Gabor patch in the receptive field) information. They showed that the neural latency can predict the subjects' reaction time better than firing rate can.

1.3. Neural Latency and Decision

The results of Lee et al. (2010) suggests that the V1 neurons, that are thought to lie at a relatively low hierarchical position along the whole axis of visuomotor processing, influence the behavioral outcome. This can be understood as the variability of the neural latency that influenced the onset of accumulation of decision units. Furthermore, one can hypothesize that the latency of information processing influences the direction of decision.

Let's imagine a situation in which more than two accumulators compete against one another, and each one of them has a different direction of decision. For example, unit A contribute to make a decision that the visual stimulus is oriented to 90 degree, whereas unit B does the same for 0 degree orientation. If visual stimulus of 0 degree orientation is presented, unit B receives a more intense information updates from input source, resulting in a faster accumulation of evidence and thus, earlier crossing of the

decision threshold. But when visual stimuli lie in 45 degree orientation, both units A and B receive a weaker input from their sources. In this case, decision of the one that crosses decision threshold faster than others will be chosen as the final output of the whole system. Assuming that the rates of information accumulation in all decision units are similar, the time spent for processing the information may influence not only reaction time but also direction of decision. Thus, neural latency may predict direction of decision.

1.4. Temporal Order Judgment Task

To investigate the effects of neural latency on direction of decision, the most direct way is to alter the latency itself, which is difficult to experimentally achieve. However, manipulating the properties of physical stimuli presented to the system can induce a similar effect. Temporal order judgment (TOJ) task is one such paradigm, often combined with 2-alternative forced choice (2AFC) between asynchronous stimuli of a variety of sensory modalities, is widely used to test the temporal order discriminability in human subjects.

Besides direct manipulation of the latency with changing stimulus onset asynchrony (SOA), simplicity of the task enables participation of non-human primates as subjects. In addition, stimulus intensity, which is thought to directly affect the rate of information accumulation in decision making process, can be simultaneously controlled so that outcome behavior can be effectively evaluated. Furthermore, by presenting the

physical stimuli simultaneously, it is possible to observe whether natural variability of stimuli processing latency modulates to perceptual decision.

The aim of the current study was to develop and establish a behavioral paradigm in non-human primates that will allow experimental analysis for the relationship between neural latency and choice.

2. Methods

2.1. Subjects

Two adult male monkeys (DS: 12 years old, 7.4kg and IR: 11 years old, 7.56kg, both *Macaca Fascicularis*) participated in this study. Before this experiment, subject DS had also taken part in other experiments that involve cell recording. They were trained to perform the task for several weeks before the main experimental sessions. Overall, subject DS participated in the main experiment for 26 days and subject IR for 14 days. The length of daily data gathered from the subjects varied widely due to unstable motivation of the subject. On average, they maintained their concentration about 2~3 hours per experimental session. Animal colony was ventilated with filtered air (HEPA filter) under constant temperature and humidity (temperature: 25C, humidity: 50~60%). All the experimental procedures involving the animal were approved by the Seoul National University Animal Care and Use Committee.

2.2. Animal Surgery

An aseptic surgery was performed for implanting a head post that was later used to restrain the animal's head during experimental session. Injections of ketamine hydrocholoride (0.5mg/Kg, Yuhan Co., Korea) and atropine sulfate (0.1mg, Jeil Pharm. Co., Korea) were intramuscularly made to sedate the animal and to improve breathing.

Then, sodium thiopental (0.5mg/Kg/h, Choongwae Pharm. Co.) was intravenously administered through a catheter intubated into a lower leg vein to main anesthesia. The animal's head was mounted on a Horsley-Clarke stereotaxic frame (David Kopf Instruments, USA) after a deep anesthesia was induced. Animal's body temperature was maintained at 37℃ with the aid of a regulated heating pad (TR-200, Fine Science Tool) throughout the surgery.

2.3. Head Post implantation

On the stereotaxic frame, the shaved skin was cleaned with povidone-iodine (Betadine) scrub solution, and scalp was incised anterior-posteriorly and spread to expose the skull. After bleeding stopped, 8~10 titanium T-shaped or bone screws were placed into the skull. Then, custom-made cylindrical post made of titanium alloy was mounted on the skull and firmly affixed with a mixture of X-ray opaque bone cement (Palacos R, Biomet Merck Cementing Technologies AB, Sweden) and Vancomycin hydrochloride (Sam Cheon Dang. Co., Korea). The position of head post was AP 10mm, ML 0mm in the Horsely-Clarke stereotaxic coordinate. When the cement hardened enough, incised edge of scalp was sutured.

2.4. Animal Training

Subject DS was naive to the experiment setup whereas subject IR was well-acquainted with the environment. Thus, training time for subject DS was much longer than that for subject IR.

2.4.1 Adaptation to Experimental Environment

Subject DS began his training with climbing up a monkey chair and sitting on the apparatus for a while. As the subject was adapted to sitting posture on the chair, it was taken out from the holding room and exposed to recording chamber environment where actual experiments were to be performed. We checked whether the animal was adapted to the environment or not by offering his favorite fruits. When the animal accepted and began to eat the offerings, it was taken as a sign of adaptation.

The next phase of behavioral training ensued while the animal's head was fixed in the recording room. The animal learned to fixate on a dot on the center of a computer monitor. A drop of juice was given as a reward when the animal coincidentally stared at the fixation point. The size of fixation point was gradually reduced to guide the animal's gaze direction toward center of the monitor screen. After fixation behavior was acquired, a circular Gabor patch was presented at random peripheral position and the animal was rewarded when it made a saccade to the peripheral target after fixation offset. It took about 3 months for subject DS to go through the training described above and be

prepared to learn the main experiment task.

2.4.2. Main Experiment Task

As soon as the subject was accustomed to experimental procedures, training session for the main experiment session started. The goal was to train the subject to make a saccade toward one of two identical Gabor stimuli with SOA. To facilitate this training, the contrast and SOA of stimulus were systematically manipulated. First, the animal was asked to saccade to a single target presented after fixation period and rewarded when it directed saccade properly toward the target. When the gaze crossed the electronic window about the target, it was considered to be a correct saccade.

When animal was able to perform the task, the second visual stimulus with a large SOA (>200ms) and a low contrast (<=2%) began to appear on each trial. The large SOA and low contrast were initially introduced to help the subject to learn the task and to discriminate the earlier one. As the animal learned to saccade toward the earlier target, despite of the appearance of another stimulus, the contrast of the second stimulus was gradually increased manually by the experimenter. When the contrast level reached to that of the target, the SOA started to be shortened gradually down to 10 ms. When animals were able to perform the TOJ with the SOA of 10 ms, it was considered that training was completed.

It took about 3 months for subject DS to acquire this performance of discriminability, and about 2 weeks for subject IR. This difference in training period

seems to be due to the difference in the amount of previous participation between the two monkeys.

2.5. Experimental Setup

Two computers were used for stimulus presentation and data acquisition processes. Both computers handled the processes with the programs written in Matlab (The Mathworks, Inc.) using Psychophysics toolbox. One (Master: Intel 3.0GHz, memory 2GB, Matrox Parhelia 128MB 400Hz) was dedicated for generation and presentation of stimulus and reward control. The other one (Slave: Intel Pentium IV 3.0GHz, 2GB memory) dedicated for data acquisition and real time display of incoming data. The DAQ Toolbox (The Mathworks, Inc.) was used for the data acquisition process for the Slave computer. The two computers were connected with each other through the TCP/IP port, which allowed real time communication and synchronization of information between the computers.

Stimulus was generated in the Master computer. When a proper command was given, the Master computer displayed the visual stimulus. The screen command was duplicated by a monitor distributor (PMS-2048, Palmi System) to a 24-inch flat CRT monitor (Sony GDM-FW900, 413X310mm, 800X600 pixel, 100Hz) for the animal, and to another monitor for experimenter. The animal was placed at the distance of 77.6cm from the center of the monitor. The CRT monitor spanned ±13.1 degrees in horizontal and -11.9~ +10.5 degrees in vertical directions. The Slave computer began to sample the

signals related to the horizontal and vertical eye positions and neural activity at a rate of 25kHz with a resolution of 16-bits (NI-DAQ PCI 6013, National Instruments) at the same time when the Master computer began to present visual stimuli. The output from a photodiode (GaAsP G1115, 410-690nm, Hamamatsu Photonics, Japan) facing a central part of the left margin (50X50 pixels) of the computer monitor was also sampled at the same rate.

2.5.1. Stimulus Presentation

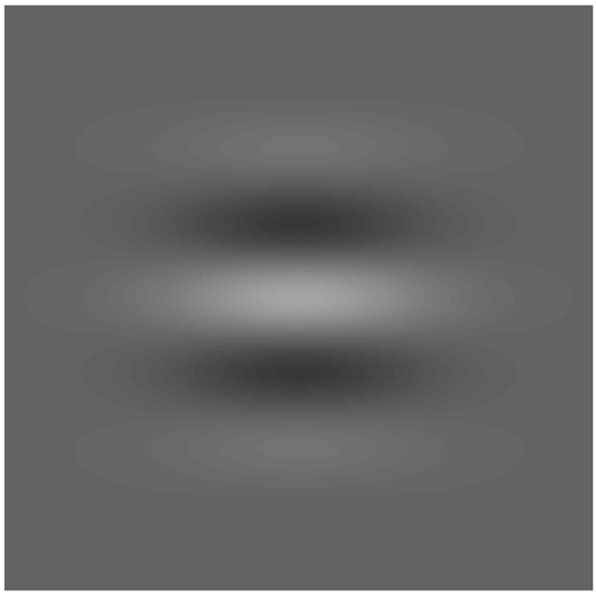

Figure* 2.** ***An example of a circular Gabor patch made by the same computer algorithm used in the current study. If this figure is sized down to 1.8 deg X 1.8 deg when viewed from 77.6cm distance, the Gabor patch will occupy 1.5 degree in visual angle.

The visual stimuli used in the current study were circular Gabor patches. The Gabor stimulus was created by convoluting a rectangular sinusoidal grating of a high contrast (64%) with a 2D Gaussian envelope. The stimulus was presented on a grey background (10.512 cd/m^2). The diameter and phase of the stimulus was set to 1.5 degree and 0 degree, respectively, for both monkeys. For subject IR, the spatial frequency and orientation were fixed to 3 cycles per degree and 0 or 90 degree, respectively. Horizontal and vertical positions of the stimulus were set to be 5 and 0 degree, respectively. For subject DS, on whom unit recording was simultaneously performed, those properties varied with the cell's preference under study. In all cases, the positions of the two stimuli, whose temporal order was to be judged, were symmetrical to the vertical axis of fixation point. Fixation point was a red dot with a diameter of 0.2 and presented at the center of CRT screen.

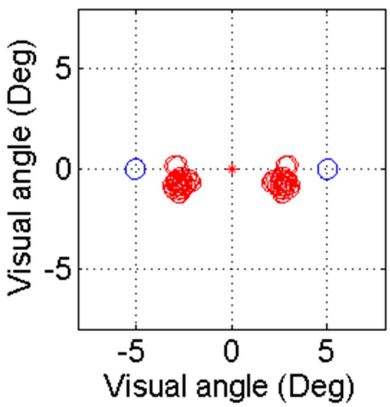

Figure 3. Target locations for subjects DS (red) and IR (blue). A red asterisk represents fixation point. For subject IR, target location was fixed at 5 degrees along the horizontal meridian. For subject SD, target locations varied day to day such that

the receptive of the cell under study was covered by one of Gabor stimuli, spanning from -3.05 to -2.11 deg horizontally and from -1.24 to 0.17 deg vertically. The size of the eye window was adjusted to avoid overlapping between the windows of the fixation and saccadic targets.

2.6. Eye Tracking Device

Horizontal and vertical eye positions of the monkey were measured with an infrared video camera (230Hz, ET-49B, Thomas recording, Germany) with an infrared LED illuminator from the right eye of the animal. The bound of the pupil was detected by thresholding a raw B/W image of the right eye and the center point of the detected boundary was calculated and eye position data (Centroid of pupil) were sent to the Master and Slave computer. The nominal delay of 7 ms for the signal related to the eye position to appear at the analog output of the eye tracker was compensated during off-line analyses.

2.7. Calculation of Eye Position

Eye position signals sampled from the infrared camera had arbitrary voltage values. Calibration was made to convert these signals into visual degree and to align the signals with pre-defined calibration by applying gain and offset value to the horizontal and vertical signal separately following the linear transformation described below:

$$EyePosH(deg) = (rawSignal(H) + Offset(H)) * Gain(H)$$

where rawSignalH means horizontal eye position signal from the eye tracker and EyePosH means transformed horizontal eye position signal.

The process consisted of two steps. First, calibration-by-pursuit method (calibration using moving objects) returned rough gain and offset value. Second, calibration-by-fixation method (calibration using flickering objects) provided more precise calibration results.

During calibration-by-pursuit, a small image (0.38 deg x 0.38 deg) of a banana or an apple moved slowly on the CRT screen for the animal to track with smooth pursuit eye movement. Pursuit movement was continually rewarded. Experimenter monitored the subject's eye movement and registered the eye position when it was aligned with the moving image. This provided rough estimates of gain and offset values.

The same images of banana and apple were used in calibration-by-fixation method. In this method, the images flickered at predefined position (e.g. -10, -5, 0, 5, 10 degree along horizontal axis) and the animal was rewarded when it fixated inside a fixed sized eye window around the flickering image. When the monkey fixated on an image, experimenter registered the eye position signals. Precise gain and offset values could be obtained with this method.

2.8. Experimental Procedure

2.8.1. Trial Sequence

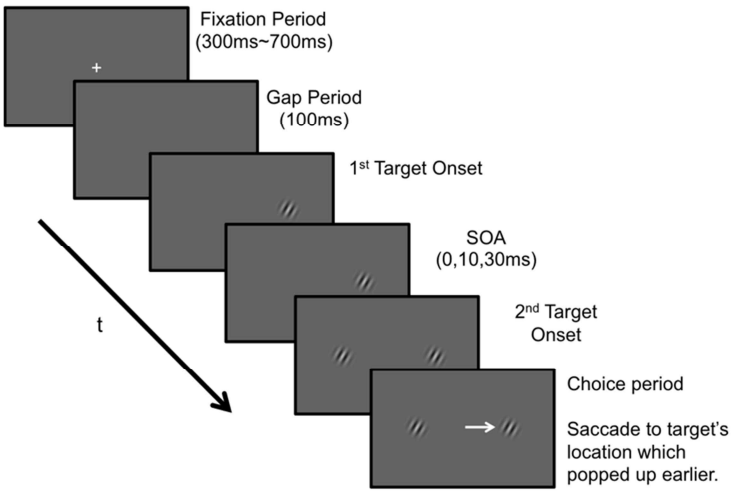

Figure 4. A trial sequence of stimulus presentation. When the animal gazed on fixation point, randomly assigned fixation period began. If animal maintained its gaze inside the eye window during fixation period, gap period began. During the gap period of 100 ms, nothing but grey background was visible. After the gap period, a target appeared at assigned location. With a SOA, the second target appeared at a mirror-symmetric location across fixation. When the assigned SOA was 0, both targets appeared simultaneously. The animal was allowed to saccade beginning at the time when the first target appeared. When the animal made a saccade, the trial ended. Note that when the animal broke the eye window before the onset of the first target, trial was immediately aborted.

A trial began with fixation point onset on a grey background together with a brief beep sound. When the monkey gazed on the fixation point, randomly assigned fixation duration began. If monkey maintained its gaze inside a circular eye window

around the fixation point until the end of fixation period, the fixation point went off and a gap period of 100ms began. After the gap period, saccade target was presented. In SOA ≠ 0 conditions, a Gabor patch popped up at one target position. Another target appeared after a SOA and the two targets remained on the screen. Targets were turned off when the animal made a saccadic eye movement toward the target that appeared earlier than the other. If the animal made a correct choice, a few drops of juice were given as a reward. If it didn't, no reward was given. In the trials with the SOA of zero, both targets appeared simultaneously, and the animal was rewarded in randomly chosen half of the trials after it made a saccade, regardless of its direction. Next trial began after an inter-trial interval of 1000 ms.

2.8.2. SOA Conditions

Three different levels of SOA (0, 10, 30 ms) were tested in the current study. Thus, five trial conditions were tested in terms of the SOA: -30, -10, 0, +10, +30ms with minus sign representing earlier target in the right side and plus sign representing earlier target in the left side. A block was composed of 20 trials and the ratio of each condition was -30:-10:0:10:30 = 1:2:4:2:1. That is, 40% of trials in a block had the SOA of zero, and other 40% of trials had the SOA of 10 ms. This ratio and small SOA were used based on animals' outstanding performance. Their sensitivity to SOA in the TOJ task was so high that the SOA larger than 10ms resulted in a ceiling effect in performance. For this reason, only 20% of trials had the SOA of 30ms to check the ceiling effect in

performance. For the trials with the SOA of zero 0, randomly-chosen half trials were rewarded, regardless of the direction that the animal chose. The order of trials in a block was shuffled randomly. A session was composed of 5 blocks in most cases, but some sessions had less than 5 blocks due to animal's unstable motivation.

2.9. Analysis

Both direction of saccade (choice) and reaction time were determined from the eye signal. In case of SOA $\neq$ 0, correct and incorrect rates were calculated. For SOA = 0, the bias in saccade direction was calculated. Psychometric functions were fitted to these data and overall bias and TOJ sensitivity were obtained. Occurrence in reward and direction of saccade in previous trials were used to test whether they had influenced animal's decision.

2.9.1. Preprocessing

2.9.1.1. Procedures

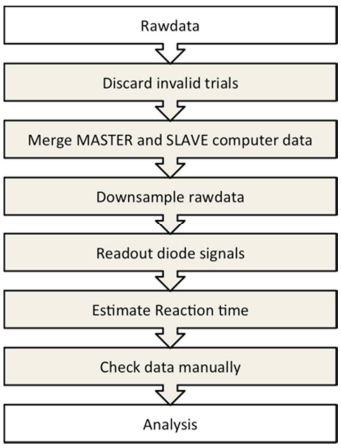

Figure 5. Flow of data pre-processing sequence. All data included in the current study went through the processes described above.

Raw data were processed through 6 steps (Figure 5). Some stages included data filtering procedures. First, trials with inappropriate animal behavior (e.g. no response) were filtered out. Second, data stored in the Master and the Slave computers were merged. The Slave computer stored most of data, the Master computer stored command tables which contained block designs, trial order, and variables used to generate and present stimulus. After the merging process, data were down-sampled from 25 kHz to 1 kHz. Originally, data sampled at 25 kHz sampling rate to extract waveforms of spikes, if there were. In the current study, however, sampling rate of 1 kHz was sufficient for analysis.

Fourth, the output signals from the photodiode were checked against the trial command information stored in the Master computer. The diode signals consisted of a series of intermittent peaks, each of which corresponded to one monitor frame that displayed visual stimuli. Computer algorithms detected each peak based on a voltage threshold. Then, it determined the SOA based on peak locations and classified trials into five SOA categories. This procedure confirmed whether the stimuli were presented properly as intended..

Finally, the eye signals combined with diode signals were analyzed and RT was calculated. RT was defined as the time from the onset of the first target to the first time point where the vectorial velocity of eye movement exceeded 15degee/sec and normal saccade followed afterwards. In order to avoid interference by noisy trace of eye velocity in this procedure, computer algorithms first searched peak velocity point in a trial and then traced back to the first point where the velocity exceeded 15deg/s. In some cases, multiple saccades were included in a trial. In that case, the saccade that crossed eye window of a fixation point and arrived at target's eye window was considered as valid saccade.

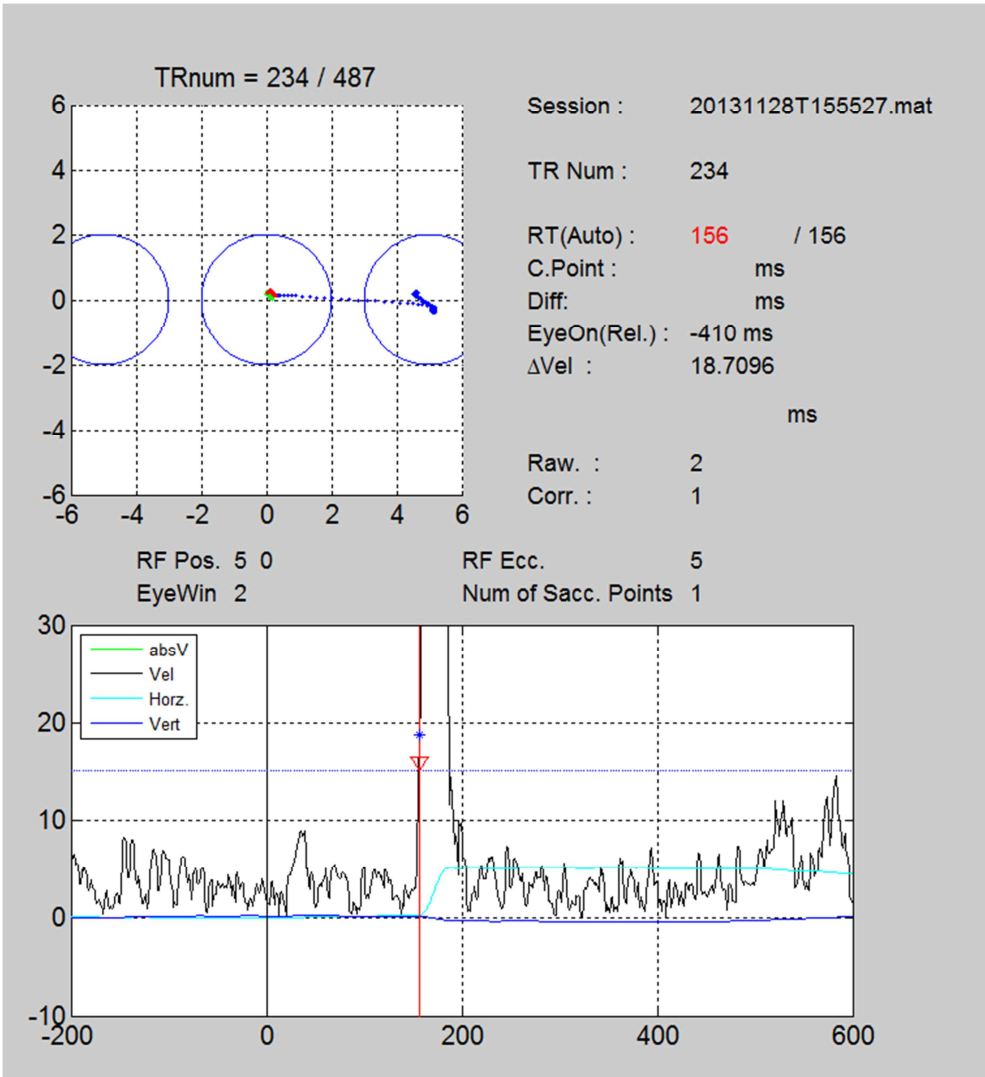

Figure 6. A captured image of RT and final check GUI panel. The panel was programmed by GUIDE function implemented in Matlab to check essential indices more easily. Indices obtained in a current trial were displayed in the upper right side of the panel. Upper: Shown is a trace of eye position during a peristimulus time period of -200 to +600 ms. X and Y axes are horizontal and vertical positions in visual angle. A blue circle in the middle represents the eye window for fixation point and those at the left and right sides represent the eye windows for saccadic targets. Each dot represents the eye position for every ms. Red, green, and blue dots are the eye positions before stimulus onset, from stimulus onset to saccadic onset, and from saccadic onset to 600 ms after stimulus onset, respectivly. Lower: Shown is eye

velocity trace (black). Horizontal (light blue) and vertical (dark blue) eye positions are also plotted. Units of Y-axis are deg/s for the velocity, and deg for position. X-axis indicates time in the unit of 100 ms with respect to the first stimulus onset point. Dotted horizontal blue line is the velocity threshold to detect the initiation of saccadic eye movement (15 degree/s). Blue asterisk is the exact point of RT on velocity trace. Red vertical line stands for calculated RT point returned by computer algorithm and inverted red triangle is the RT point that was the final output. In the case of incorrect localization of the detection algorithm, RT point was shifted to appropriate one by visual inspection.

2.9.1.2. Outliers

2.9.1.2.1. Filtering Invalid Cases

All the acquired data from the experiment went through 4 steps of data refinement procedures. First, the trials in which the animal did not respond or broke the fixation window before stimulus onset were discarded. Second, the trials signals with excessive noise artifact were excluded, as inspected by computer algorithms and then by visual inspection. Third, the trials with erroneous diode signals were discarded. This procedure filtered out the trials in which the CRT monitor failed to present stimuli on exact time, for example, gap duration longer than 100 ms or SOA longer than 30 ms, etc. Finally, RT of each trial determined by computer algorithms was checked against raw eye signals and reconstructed eye trace (Figure 6). During this procedure, the trials that survived valid saccade detection algorithm, or the trials in which the eye position error was erroneously introduced by failure of locating the centroid of pupil, were filtered out.

2.9.1.2.2. Behavioral Outlier

Saccadic RT (SRT) shorter than 40 ms were classified as anticipatory saccade and discarded. On the other hand, SRT longer than 400 ms from stimulus onset was classified as unattended cases and discarded. Details are shown in Table 1.

2.9.1.2.3. Invalid SOA

For some sessions of subject DS, trials with different size of SOA other than -30,-10, 10, 30ms existed. These trials were inserted when task performance at given SOA level was too low. These trials were excluded from further analysis.

Date	Raw Length	DAQ Artifact	Invalid Diode	Behavior Outlier	Behavior Outlier Detail		After Pre-processing	Invalid SOA	Input to Analysis
					Invalid Saccade	RT Outlier			
120830	781	0	10	15	13	2	756	232	524
120831	360	1	8	9	9	0	342	0	342
120918	800	2	8	3	3	0	787	0	787
120920	500	1	14	4	4	0	481	0	481
120921	600	0	7	9	9	0	584	0	584
120927	700	1	8	16	15	1	675	0	675
121004	800	0	6	4	3	1	790	0	790
121005	800	0	10	21	20	1	769	59	710
121016#1	455	0	3	3	3	0	449	0	449
121016#2	300	0	2	2	2	0	296	0	296
121018	800	0	6	6	6	0	788	0	788
121023	800	1	6	7	7	0	786	0	786
121025	457	0	17	2	2	0	438	0	438
130103	600	0	2	5	5	0	593	0	593
130104	700	3	5	0	0	0	692	0	692
130111	684	1	5	9	9	0	669	0	669

130115	800	7	7	2	2	0	784	0	784
130116	530	0	6	19	19	0	505	0	505
130118	687	0	4	7	7	0	676	0	676
130122	783	161	11	2	2	0	609	0	609
130205	560	0	6	4	4	0	550	0	550
130207	860	0	4	4	4	0	852	0	852
130214	700	5	4	2	2	0	689	0	689
130215	854	0	2	6	6	0	846	0	846
130219	800	2	3	2	2	0	793	0	793
130225	848	8	4	1	1	0	835	0	835
Total	17559	193	168	164	159	5	17034	291	16743

Table 1. Outlier exclusion details of data obtained from Subejct DS

Date	Raw Length	DAQ Noise	Invalid Diode	Behavior Outlier	Behavior Outlier Detail		After Pre-processing	Invalid SOA	Input to Analysis
					Invalid Saccade	RT Outlier			
130913	874	0	8	7	7	0	859	0	859
131015	744	0	4	1	1	0	739	0	739
131114	738	0	3	0	0	0	735	0	735
131119	600	0	1	0	0	0	599	0	599
131120	700	0	3	1	1	0	696	0	696
131121	939	39	5	1	1	0	894	0	894
131125	500	0	1	1	1	0	498	0	498
131126	599	0	3	0	0	0	596	0	596
131127	687	0	2	1	0	1	684	0	684
131128	488	0	1	1	1	0	486	0	486
131203	600	0	3	2	2	0	595	0	595
131204	700	0	2	3	3	0	695	0	695
131211	1180	0	6	3	3	0	1171	0	1171
131213	1200	0	6	2	2	0	1192	0	1192
Total	10549	39	48	23	22	1	10439	0	10439

Table 2. Outlier exclusion details of data obtained from Subject IR

2.9.3. Curve Fitting

Correct rates of TOJ were calculated for SOA ≠ 0 conditions. To estimate psychometric functions for each day's and overall results, correct rates were transformed into p(R), the probability of making rightward saccade under given SOA condition as following.

$$p(R)_{SOA} = \frac{Number\ of\ trials\ with\ rightward\ saccade_{SOA}}{Total\ number\ of\ trials_{SOA}}$$

Psychometric functions for each subject then were estimated using p(R). The psychometric function PF(x) was defined as below:

$$PF(x) = \gamma + (1 - \lambda - \gamma) \times f(p(R))$$

Where γ denotes for base line probability which can be obtained when animal randomly chooses each target. It was set to 0. λ is lapse rate, which represents the degree of animals' misbehavior occurring independently from TOJ sensitivity. *f(x)* is a model function to generate sinusoidal curve. During the estimation procedure, lapse rate

was set as a free parameter with no bounds and model function was cumulative Gaussian function,

$$f(p(R)) = \frac{1}{2}\left(1+erf\left(\frac{p(R)-\mu}{\sigma\sqrt{2}}\right)\right)$$

where error function *erf(x)* is defined as below:

$$erf(x) = \frac{2}{\sqrt{\pi}}\int_0^x e^{-t^2}dt$$

The data was fitted by Optimization toolbox on the Matlab (MathWorks.) using a maximum-likelihood method. The algorithm compared the observed p(R) and estimated p(R), and tried to minimize their deviance in each iteration. The iteration stopped when the deviance reached local minima. The estimation results of each session and subject were checked manually to prevent the algorithm from falling in inappropriate minima of deviance. p(R) for SOA = 0 condition was not entered in fitting procedure.

2.9.4. Reaction Time Comparison

Reaction times of each animal were calculated and compared between

conditions. As the distributions of reaction time were skewed, both mean and median of the distributions were used to compare the distributions. In each condition, reaction times of correct and incorrect trials were calculated separately. Statistical differences between the mean of distributions were calculated using 2-sample t-test under the assumption of unequal variance.

2.9.5. Bias Comparison

Bias in animal's saccade direction can be expressed in two ways. One way is to estimate psychometric function and compare derived parameter, such as mean of the fitted curve when using cumulative normal function for fitting procedure. Another more direct way is to compare the ratio of saccade direction in SOA = 0 condition. In the current study, both indices were calculated and the relationship between them was examined.

2.9.6. Reward History Analysis

If any bias existed in animal's behavior when choosing the direction of saccade, one possible explanation for it is that the rewards of past trials may have biased the animals' behavior. This can be confirmed by investigating the reward history of n^{th} trial. However, if animal noticed a definite SOA in n^{th} trial, the decision made in the trial was rather influenced by perceptual cues (SOA), not reward history. To eliminate this

possibility, only the n^{th} trials in SOA=0 condition were considered when analyzing reward history. Rewardedness of a trial was coded ‘1’ if animal was rewarded in certain trial, ‘0’ if not. And also, the direction of saccade was coded ‘1’ for rightward saccade, and ‘-1’ for leftward saccade. To present rewardedness and direction of saccade in a single index, values were multiplied so that only the rewarded saccades were marked either ‘-1’ or ‘1’.

Since they were not quantities, but dummy variables coding qualities (that is, nominal variable) with 3 categories, multinomial logistic regression method using multinomial logit model was applied to quantify and test statistical significance of the effect of previous reward on saccade direction. The algorithm was adopted from Statistics toolbox of the Matlab (The MathWorks). Number of trial order, K, i.e., the number of indicator was set to 5 for daily or session-wise analysis. Accuracy of prediction was calculated by comparing predicted with actual choices.

3. Results

3.1. Data Description and Curve Fitting

Subject	Days	Sessions	Blocks	Trials	SOA conditions (ms)					Choice	
					-30	-10	0	10	30	Left	Right
DS	26	202	886	16743	1634	3315	6835	3298	1661	8977	7766
IR	14	110	530	10439	1035	2077	4189	2101	1037	6236	4203
	40	312	1416	27182	2669	5392	11024	5399	2698	15213	11969

Table 3. Summary of data obtained from both subjects.

For both monkeys, a total of 27182 valid trials were collected. Subject DS participated in more trials than subject IR, but average of successful trials per day are slightly higher for IR (DS = 643.96, IR = 745.64). Uneven distributions of trials across conditions are due to proportion of trials assigned to each condition and outlier screening procedures (see Method). Overall, both animals had a tendency to choose the left target over right one. More detailed comparison will be dealt with in following sections.

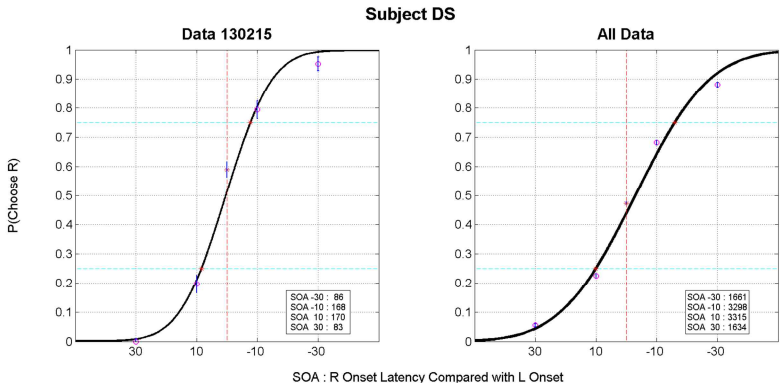

Figure 7. Estimated psychometric function of Subject DS. Left curve is from the data 130215, and the right one is from overall data from this subject. Blue dots represent calculated p(R) at each SOA and thick sold black line is a sigmoid curve derived from estimated psychometric function. Red dashed line in the middle shows SOA=0 point on X-axis. Insets show number of trials of corresponding SOA. Blue horizontal lines on each figure represents 25%, 75% percent of p(R).

Figure 7 Shows fitted psychometrics curves from data gathered on 130215 (left) and all data (right) obtained from subject DS. p(R)s for each SOA condition were calculated and entered in fitting algorithm. Inputs to the algorithm are shown in Table 4. As already noted in Method, the condition of the SOA of 0 was omitted in psychometric function estimation. Table 5 shows the results from two estimations. Data from the 130215 showed a nice performance, as animal's choices were not biased toward one side and perceptual threshold for SOA detection was lower than 10ms, which is smaller than the minimum SOA that could be produced by experimental device used in current study. However, overall data reveal that the animal's PSE was biased toward the left side by about 3ms. Also, both upper and lower threshold to detect SOA were larger than those of psychometric function estimated from 130215 data.

	Observed Value	SOA (ms)			
		-30	-10	10	30
Data 130215	P(R)	0.000	0.196	0.794	0.952
	Std.	0.010	0.031	0.031	0.024
	N	86	168	170	83
All Data	P(R)	0.055	0.226	0.681	0.881
	Std.	0.006	0.007	0.008	0.008
	N	1661	3298	3315	1634

Table 4. Input values entered for estimation of psychometric function for Subject DS

Est. Parameter (ms,)	Mean	Std.	Upper Th.	Lower Th.
Data 131126	-0.38	11.94	7.72	-8.41
All Data	2.90	19.27	15.90	-10.09

Table 5. Output values from estimation of psychometric function for Subject DS

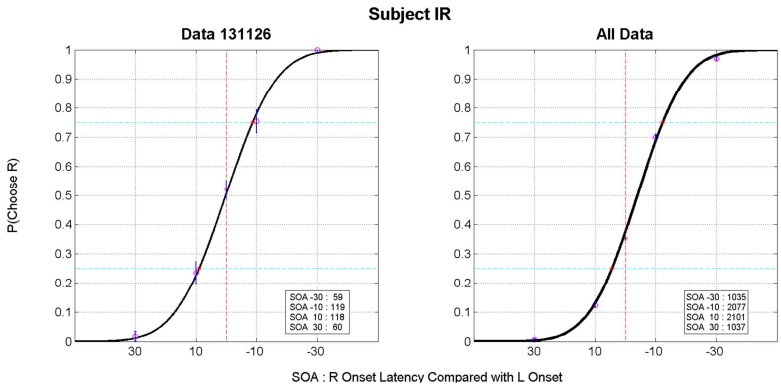

Figure 8. Fitting results for subject DS. Results from representative data 'Data 13126' are shown in the left panel and results from all data are shown in the right panel. Same convention as Figure 7.

This trend could be also found in subject IR's data, and even more exaggerated. Compared to the sigmoid curve derived from data 131126, the curve from IR's all data is heavily shifted toward the right side. This means that the animal perceived the left target to have appeared earlier. Both animals' biases show a similar tendency. In summary, both animals showed a great performance within a few sessions, but developed a leftward bias.

	Observed Value	SOA (ms)			
		-30	-10	10	30
Data 131126	P(R)	0.017	0.235	0.754	1.000
	Std.	0.017	0.039	0.040	0.010
	N	59	119	118	60
All Data	P(R)	0.007	0.123	0.700	0.970
	Std.	0.003	0.007	0.010	0.005
	N	1035	2077	2101	1037

Table 6. Input values entered for estimation of psychometric function for Subject DS

Est. Parameter (ms,)	Mean	Std.	Upper Th.	Lower Th.
Data 131126	-0.019	1.308	0.863	-0.901
All Data	0.393	1.240	1.229	-0.443

Table 7. Output values from estimation of psychometric function for Subject IR

3.2. Reaction Time Comparison

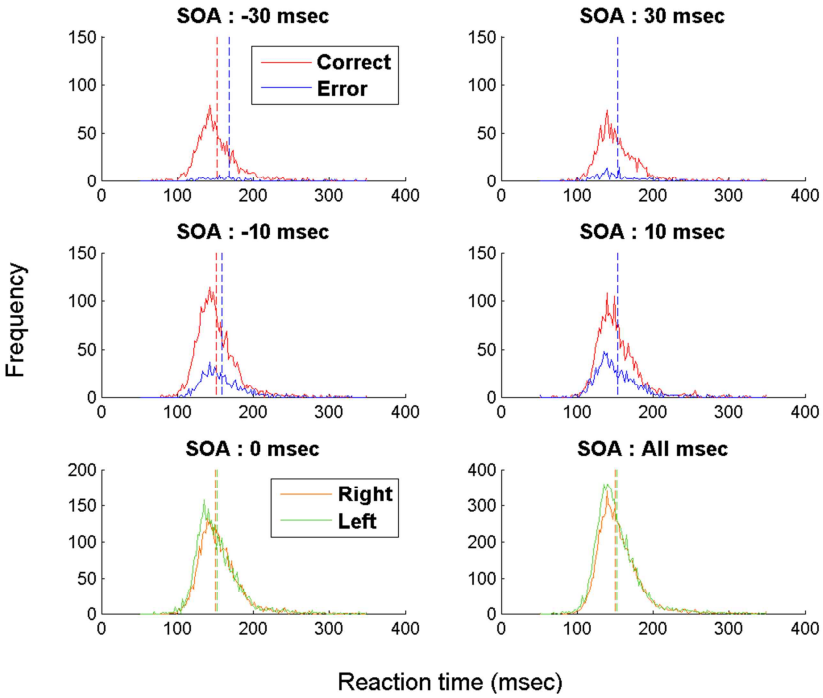

Figure 9. RT distribution of Subject DS under different conditions. The distributions are plotted separately according to SOA. Red curves indicate distributions from correct trials and blue curves from incorrect trials. For SOA of zero and all SOA conditions, trials are grouped according to saccade direction. Yellow curves indicate distribution from rightward saccade trials and blue curves from leftward saccade trials. Dashed vertical lines represent the mean of the distribution.

Distributions of SRT from subject DS are depicted in Figure 9. It is easy to notice that the number of error trials is small in large SOA conditions (91 cases for -30ms SOA, 195 cases for 30ms SOA). This is because animal seldom made an error under those conditions. For SOA < 0 conditions (-30, -10ms SOA), means of correct and

error distributions are different as error SRT distributions' means are falling behind. These difference are statistically significant (Figure 10, $p<0.05$). The mean SRT differences are 16.13ms for -30ms SOA condition and 7.62ms for -10ms SOA condition. Similar pattern was not observed for SOA > 0 conditions.

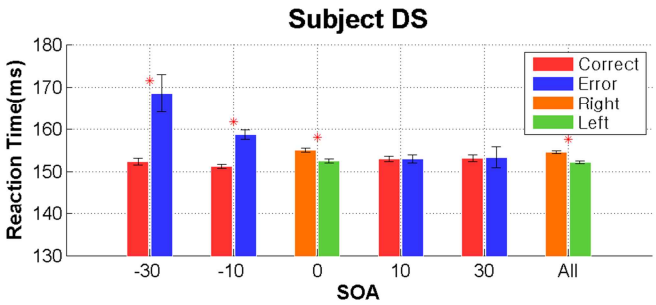

Figure 10. Comparison of mean RT of Subject DS under different SOA conditions. Trials with the SOA of 0 and all SOA conditions are grouped by their saccade direction and means of both groups are presented separately. For other 4 conditions, trials are grouped by correctness. Error bars represent standard error of mean. Red asterisks indicate that the difference of means from two groups are statistically significant (2-sample t-test, p<0.05).

SOA (ms)	Correctness	Mean RT	Std RT	Median RT	# of Case
-30	Correct	152.31	28.72	147	1570
-30	Error	168.44	42.52	160	91
-10	Correct	151.19	27.33	147	2554
-10	Error	158.72	30.32	153	744
0	Left	155.17	28.52	150	3233
0	Right	152.72	30.01	147	3602
10	Correct	152.93	28.13	148	2259
10	Error	152.99	31.34	146	1056
30	Correct	153.12	28.71	148	1439
30	Error	153.31	34.14	146	195

All	Left	154.63	28.91	150	7766
All	Right	152.26	29.31	147	8977

Table 8. Mean, standard deviation, and median of RT distributions of Subject DS

The SRT difference between two saccade direction with the SOA = 0 condition is 2.54 ms and statistically significant ($p<0.05$). This pattern of difference is still observed for each distribution. Note that in all histograms, the shape of the distributions is unimodal and skewed positively.

SOA (ms)	t_value	p
-30	-3.57	0.0006
30	-0.07	0.9408
-10	-6.09	1.53323E-09
10	-0.05	0.9566
0	3.47	0.0005
All	5.27	1.36279E-07

Table 9. Results of 2 sample t-test of correct and error RT groups of Subject DS

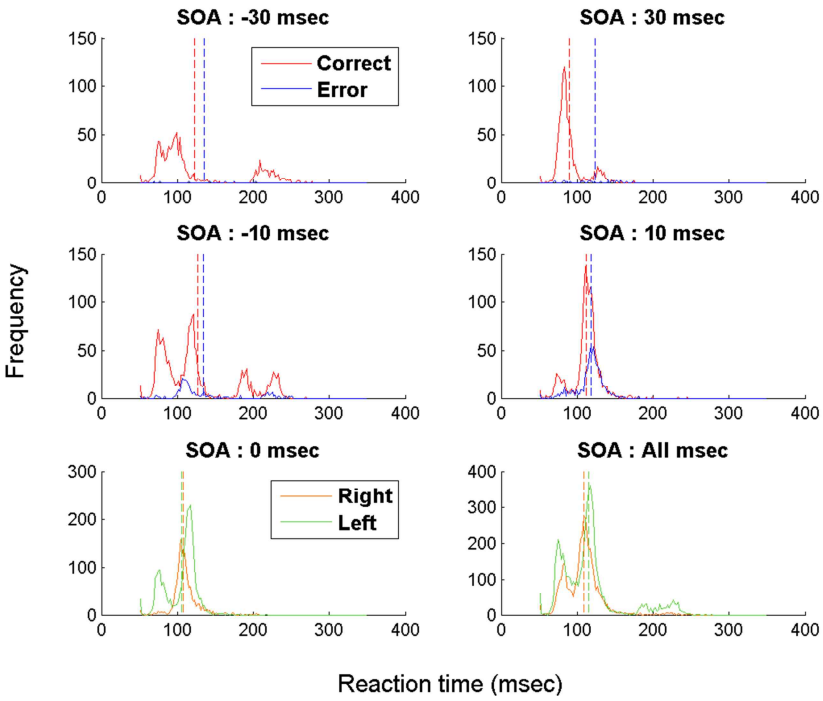

Figure 11. RT distribution of Subject IR under different conditions. Same convention as Figure 9.

In IR's SRT histograms, however, distinct features can be noticed. First, unimodality of SRT distribution is rarely observed. Rather, bimodal and quad modal (correct cases in -10 SOA condition) can be found. The pattern seen from subject DS that error trials mean RT is slower than correct ones is also observed in subject IR with the SOA of -30,-10,10,30ms. Except for the difference found in – 30ms SOA condition, all other differences are statistically significant (Table 10, $p<05$). Compared to subject DS, the mean RT difference between correct and incorrect trials is seen in both directions of saccade. For the SOA of zero and all SOA, the pattern of mean RT

difference is inverted. Leftward saccades were faster in zero SOA condition, whereas rightward saccades were faster in all conditions on average and both differences were statistically significant. This pattern, however, may come from the inadequacy of mean as a proper index for the central tendency of distribution, as it is not robust when the distribution shows multimodal properties. Due to the multimodality of distributions, standard deviations of RT are much bigger than those of subject DS.

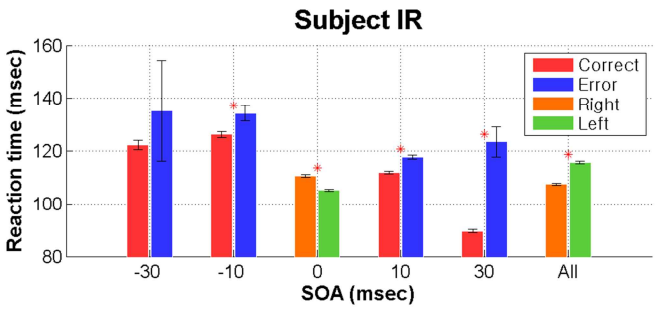

Figure 12. Comparison of mean RT for Subject IR under different SOA conditions. Same convention as Figure 10.

SOA (ms)	Correctness	Mean RT	Std RT	Median RT	# of Case
-30	Correct	122.37	56.02	99	1030
-30	Error	135.29	50.24	143	7
-10	Correct	126.29	50.43	116	1842
-10	Error	134.26	46.72	114	259
0	Left	110.65	17.31	108	1479
0	Right	105.20	21.22	112.5	2710
10	Correct	111.80	19.04	114	1454
10	Error	117.78	17.82	120	623
30	Correct	89.61	17.57	85	1004

30	Error	123.45	31.33	124	31
All	Left	107.52	23.96	109	4203
All	Right	115.61	39.87	113	6236

Table 10. Mean, standard deviation, and median of RT distributions of Subject IR

As the RT distributions showed different patterns, it was safe to continue analysis without pooling the animals' data as the two dataset might have followed distinct TOJ mechanisms. Thus, the results from all analyses in the current paper will be shown separately for individual subject.

SOA (ms)	t_value	p
-30	-0.68	0.5230
30	-5.98	1.35136E-06
-10	-2.55	0.0113
10	-6.87	1.01997E-11
0	8.98	4.28439E-19
All	-12.94	0.0000

Table 11. Results of 2 sample t-test of correct and error RT groups of Subject IR

3.3. Bias Comparison

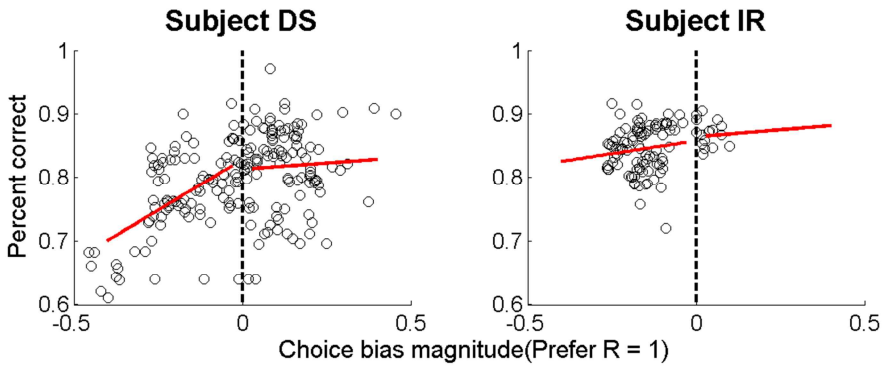

Figure 13. Scatter plot of percent correct and choice bias for subjects DS and IR. For both figures, X axis shows the degree of choice bias and Y axis shows percent correct. Zero point on the X-axis or the vertical dashed line means that the animal chose left and right targets equally under SOA zero condition in a given trial. Positive value of choice bias means rightward saccade was more frequent, and negative value means the opposite. Red lines on the left and right halves of each plot represent regression lines calculated with data points on each half of the plane. Indices are calculated from each session.

As described above, both animals showed an overall leftward bias of choice across conditions. It is possible that motivational depletion might have led the animal to make a saccade toward one direction to minimize any effort regardless of SOA. Thus, the magnitude of bias may be correlated with animal's correct rate. Figure 13 shows scatter plots of choice bias against correct rate in each session for each subject. Note that p(R) for SOA = 0 condition is used as choice bias index as it does not depends on any other performance related values. Black dashed line is no-bias line (choice bias = 0). The data are separated by no-bias line to show direction-wise difference of pattern

between choice bias magnitude and correct rate. Positive value of x-axis means data represented by the point is biased toward rightward saccade and negative values for the leftward saccade. Red solid lines are regression lines for each side of data.

Overall, similar trends were observed for both subjects. Pearson correlation coefficients for all, left and right side data of subject DS are shown in Table 11. Positive correlations are found in all and left side data. ($p < 0.05$) However, right side data show no significant correlation with correct rate. Linear regression coefficients for left side data was 0.32 (p= 1.37e-09) and for all data was 0.17 (p = 2.35e-11). For the subject IR, only the correlation between choice bias and correct rate in all side data was significant. As the subject IR showed a heavily biased response toward leftward target (number of negative choice bias index of 93 vs that for positive bias index of 14), and a relatively large p-value of correlation coefficient for the right side data might have come from the small sample size. Details are shown in Table 12.

Side	R	p	N
All	0.45	2.35E-11	202
Right	0.05	0.5859	107
Left	0.57	1.37E-09	95

Table 12. Correlation analysis results of percent correct and choice bias magnitude for Subject DS.

Side	R	p	N
All	0.27	0.0047	107
Right	0.06	0.8367	14
Left	0.12	0.2372	93

Table 13. Correlation analysis results of percent correct and choice bias magnitude for Subject IR.

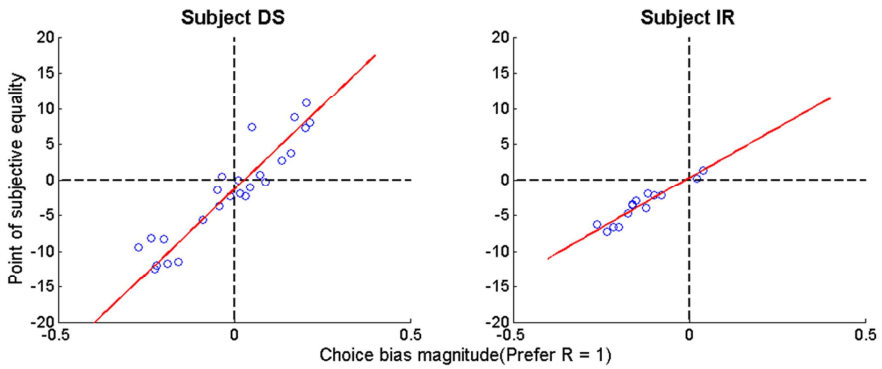

Figure 14. Scatter plot of two bias indices (p(R) and PSE) for both subjects. Number of data points is far less than Figure 13 as PSE could be estimated from a day's trials. Red sold lines are linear regression lines for both data. Both PSE and P(R) of SOA of zero, positive values mean that choices are biased toward the right side and negative means the opposite.

Relationship between choice bias from SOA = 0 and point of subjective equality (PSE) from psychometric function is shown in right panel of Figure 16. It seems clear that those two indices are well correlated for both subjects. For the subject DS, Pearson correlation coefficient for the two bias indices is (R=0.93, p =3.77e-12). Although those two indices are based on different sets of data, the biases show a similar trend. For the subject IR, the correlation between two bias indices showed a strong and significant relationship between two values (R =0.95, p =3.06e-07). Also, the linear regression coefficient beta for all data was 0.11 (p= 0.0047).

3.4. Reward History Analysis

	Distance K from Nth trial									
	N-1	N-2	N-3	N-4	N-5	N-6	N-7	N-8	N-9	N-10
1	0.210									
2	0.205	0.159								
3	0.203	0.160	0.147							
4	0.204	0.159	0.147	0.096						
5	0.205	0.159	0.144	0.092	0.064					
6	0.209	0.159	0.142	0.090	0.064	0.041				
7	0.209	0.156	0.143	0.088	0.062	0.039	0.079			
8	0.206	0.161	0.143	0.088	0.060	0.038	0.080	0.072		
9	0.205	0.159	0.146	0.087	0.058	0.037	0.076	0.071	0.096	
10	0.207	0.158	0.143	0.087	0.060	0.038	0.074	0.068	0.097	0.056

Table 14. Coefficient beta estimated from logistic regression for Subject DS. Each number in cell represent estimated coefficient from logistic regression analysis. Header of each row shows number of indicators included in logistic regression model and header of each column shows that coefficient of the column belongs to the predictor from N-k trials reward history.

Table 13 shows regression coefficients for indicators. Coefficient values in red are statistically insignificant ones ($p<0.05$). The results show that rewardedness is not helpful to predict current trials choice when K increases as corresponding coefficient gradually becomes smaller. Except for 6^{th} indicator in models with more than 7 indicators, all other indicators are statistically significant. Accuracy of predictions for each different model with different indicator numbers are shown in the left panel of Figure 15. Accuracy generally increases as the number of indicator increases. The magnitudes of accuracy were under 60% for all models. For 5-indicator model, coefficient gradually decreased as K increased (right panel of Figure 15), indicating that

recent trials had more effects on the choice of current trial.

As the effect of reward history may differ by day or session, the accuracy for each session or day was calculated. The results are shown in Figure 16 by histograms of accuracy.

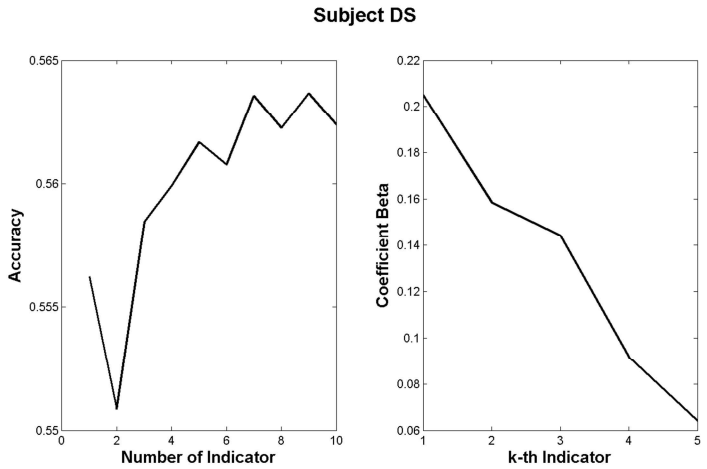

Figure 15. Results from logistic regression analysis using Subject DS data. (Left) Calculated accuracy of prediction as a function of the number of indicators entered in logistic regression model. X-axis shows the number of indicators, i.e., the number of trial order considered in the model, and Y-axis shows calculated accuracy of a given model. Note that Y-axis is scaled to show the trend of change in accuracy. (Right) Coefficient beta of K-th indicator. X-axis means k-th indicator and Y-axis means corresponding coefficient beta for the indicator.

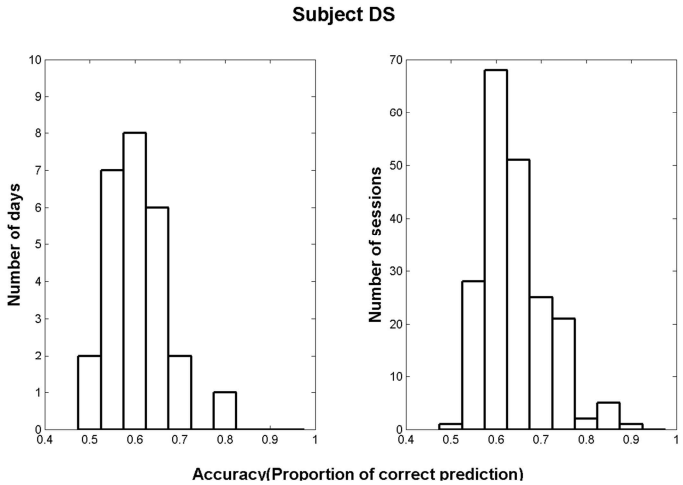

Figure 16. Histograms of prediction accuracies of logistic regression models. (Left) Accuracy calculated for each day. (Right) Accuracy calculated for each session. Note that baseline probability from randomly made decision is 0.5 for both histograms.

For 26 days, mean of accuracy was 0.61 and standard deviation was 0.06, indicating that the performance was better than the chance level accuracy (0.5) by about 10%. The average number of statistically significant coefficient was 1.71. For 197 sessions, mean accuracy was 0.64 and standard deviation of accuracy was 0.07. Average number of statistically significant of indicator was 0.65, even shorter than day-wise analysis.

	Distance K from Nth trial									
	N-1	N-2	N-3	N-4	N-5	N-6	N-7	N-8	N-9	N-10
1	-0.364									
2	-0.370	0.010								
3	-0.369	0.015	0.041							
4	-0.372	0.012	0.043	0.005						
5	-0.373	0.011	0.040	0.001	-0.022					
6	-0.372	0.011	0.038	0.003	-0.023	0.016				
7	-0.375	0.006	0.037	0.002	-0.024	0.012	-0.034			
8	-0.379	0.006	0.037	0.002	-0.028	0.012	-0.034	-0.029		
9	-0.377	0.005	0.029	0.001	-0.025	0.014	-0.031	-0.026	0.018	
10	-0.378	0.003	0.026	-0.001	-0.025	0.017	-0.033	-0.024	0.026	0.066

Table 15. Coefficient beta estimated from logistic regression for Subject IR. Same convention as Table 14.

Table 14, Figure 15, and Figure 16 show the results of the same analysis from the Subject IR. Notations are used in the same manner as the results of the subject DS. Unlike the subject DS, only the regression coefficients with K less than 3 were statistically significant. Also, the N-1 trials affected current n^{th} trial in the opposite way when compared to the result of subject DS. Absolute value of coefficient decreased rapidly compared to the coefficients of the subject DS. These differences suggest that the subject IR may have been influenced less by previously rewarded side and chose in a more randomized fashion than subject DS. Distributions of days' and sessions' accuracy are presented in Figure 20. For subject IR, mean of daily accuracy was 0.61 and standard deviation was 0.04. The distribution is narrower, but placed at a similar position as that of the Subject DS. The average number of statistically significant

indicator was 2.07. For 110 sessions, mean accuracy was 0.65 and standard deviation of accuracy was 0.05. The average number of statistically significant indicator was 1.25.

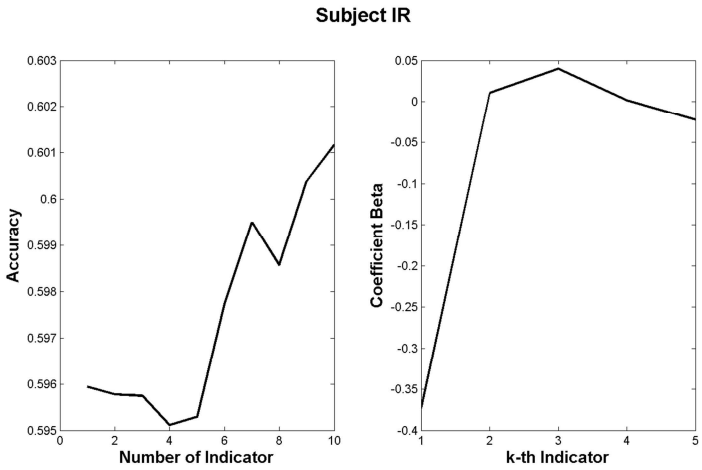

Figure 17. Results from logistic regression analysis using Subject IR data. Same convention as Figure 15.

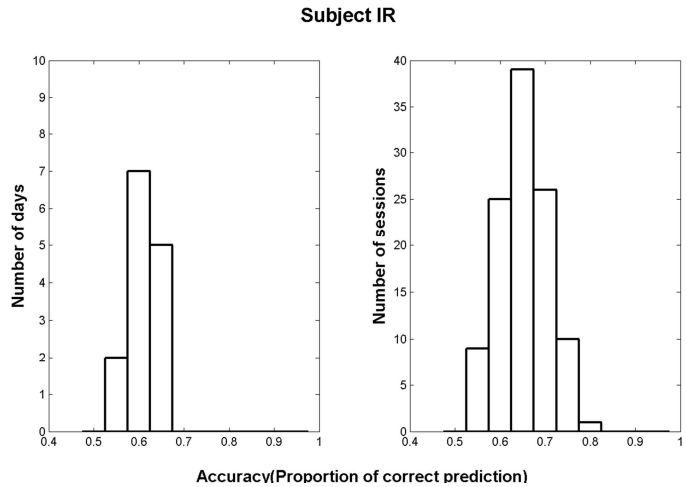

Figure 18. Histograms of prediction accuracy of logistic regression models. Results from logistic regression analysis using Subject IR data. Same convention as Figure 16.

4. Discussion

4.1. Summary

A TOJ task was developed for non-human primates. Two monkeys showed a great performance in the TOJ task, with their TOJ sensitivity near the smallest possible SOA that could be produced by experimental device. Results also indicated that there may be inter-subject differences in SRT distribution, bias pattern and dependency on reward history. Statistically significant difference in the mean SRT between correct and incorrect trials in both subjects was observed, but the conditions in which this difference was found were not identical between two subjects. Subject DS was biased toward the leftward choice when its correct rate was low, but subject IR was biased toward the leftward choice regardless of its correct rate. Also subject DS tended to choose the same side as the past trials if it was previously rewarded, whereas subject IR chose the opposite side to the past trials if it had been reward. These results suggest that subject dependent difference in choice strategy may exist in TOJ task.

The aim of the current study was to develop an experimental protocol for non-human primates that could be applied for extracellular recording experiments in future. The results obtained seem to be satisfactory as these results indicate that the animal's decision relied on multiple factors other than physical stimulus property, the SOA.

4.2. SRT distribution

Two aspects of inter-subject difference in SRT results are worthy of consideration: asymmetry in the mean RT between correct and incorrect trials and the difference in the shape of SRT distribution, especially the number of peaks in SRT distribution. The pattern of asymmetry in the mean RT between correct and incorrect trials seems to differ between subjects. In case of subject DS, a significant difference in the mean RT was only found when the right target preceded the left target, whereas subject IR's mean RTs differed significantly on both sides, except for the SOA of -30ms in which the animal made only 7 errors out of 1035 trials.

Multimodality of SRT distribution has been repeatedly reported in previous studies (Fischer & Boch, 1983; Fischer, Boch, & Ramsperger, 1984; Munoz & Wurtz, 1992; Priori, Bertolasi, Rothwell, Day, & Marsden, 1993; Rohrer & Sparks, 1993), but it seems that no clear explanations for the phenomenon are available. Although the underlying mechanisms of this phenomenon are unlikely to be revealed under this TOJ experimental paradigm, it is reasonable to suspect that multimodality of subject IR's RT distribution may reflect anticipatory saccades, as the earliest mode seems to appear less than 100ms after stimulus onset. In that case, the correct rate of the earliest mode should have been around 50%, which could be obtained when the animal randomly chose targets. However, as shown in Figure 11, the frequency of correct response exceeded that of incorrect response in every observable modes indicating that anticipatory saccades cannot account for this phenomenon. Calculating exact values of correct rate

for each individual mode seems to be meaningless, as the number of modes varied across experimental conditions.

4.3. Bias as task strategy

The pattern of bias in each subject with respect to its percent correct response suggests that the animal preferred one side when the temporal order of stimuli was uncertain. Subject IR showed a stable performance (low variance in percent correct response), yet a large bias. One possible explanation for the bias is that it could be a strategic solution under uncertainty especially when the reward was randomly given (Donahue, Seo, & Lee, 2013). Subjects' expected reward was maximized when they chose one side throughout the whole experiments, guaranteeing reward in 50% of times. However the degree of bias was not directly linked to the amount of actual reward except for the completely biased case. Subject IR showed a stronger bias than subject DS did (Table 3), the probability of reward in the trials with the SOA of zero was slightly higher for subject DS (DS = 0.4926, IR = 0.4865).

Describing choice bias as a strategic task performing behavior assumes that the bias is a product of sophisticated cognitive procedures. However, the bias could be explained at the lower level information processing stage. The left gaze bias (LGB) phenomenon is probably related to the bias observed in this study, though the generalizability of stimulus type inducing LGB seems unclear (Guo, Meints, Hall, Hall, & Mills, 2009; Mertens, Siegmund, & Grüsser, 1993; Shimojo, Simion, Shimojo, &

Scheier, 2003).

4.4. Dependency on reward history

Maybe the most noticeable inter-subject difference observed in the current study was the difference between subject in the dependency of choice of current trial on the past reward history. Logistic regression analysis showed that subject DS tended to choose the same side where previously rewarded, whereas subject IR tended to choose the opposite. Analogous to the bias pattern, this could represent the animal's unique strategy when physical cue is weak. Previous studies have reported similar results (Donahue et al., 2013), but individual difference between participants were not observed.

The distinctive features of reward history, however, were not lead to the accuracy of prediction. The accuracy of prediction was higher than chance level (i.e. 50%), but lower than the baseline prediction rate (i.e. 75%), indicating that reward history alone could not account for behavioral outcome, even though the physical cues were absent. Considering that the bias in the animals' choice was included in logistic regression equation (i.e. as intercept term), it seemed that the decision of animal was influenced by other factors than those two. It could possibly be other top-down components or the internal noise arising through the visual processing stages.

4.5. Application to cell recording experiment

The results of this study revealed that even simple discrimination task (i.e. TOJ task) can be affected by various factors from physical cues to high level cognitive strategies. Increase of number of factors may imply attenuation of the effect of visual information processing latency, which is major interest of future cell recording experiment, on decisional direction. Furthermore, most of them seem to be top-down components that are difficult to manipulate directly by experimental methods.

The effects of possible confounding variables, however, do not necessarily mean that the effect of processing latency cannot be observable. In other words, the roles of exogenous cues do not seem to be compromised completely by other factors. When exogenous stimuli were presented, the animals' choice was heavily driven by the physical cues rather than other endogenous factors. Also, they were able to judge up to the SOA of 10ms, indicating that perceptual sensitivity is sustained throughout the experiment and the animal kept focusing on the task.

Considering the factors discussed above, we could conclude that initial hypothesis about the effect of visual processing latency can still be tested under cell recording experiments. Of course, to prevent confounding factors from dissipating the effect, additional precise experimental control methods should be considered. In addition, designing the model that can quantify the factors influencing the decision and estimate their magnitude of influence on decision can help resolving the problem.

5. Reference

Becker, Gordon M, DeGroot, Morris H, & Marschak, Jacob. (1964). Measuring utility by a single-response sequential method. *Behavioral science, 9*(3), 226-232.

Carpenter, RHS. (1981). Oculomotor procrastination. *Eye movements: Cognition and visual perception*, 237-246.

Donahue, Christopher H, Seo, Hyojung, & Lee, Daeyeol. (2013). Cortical Signals for Rewarded Actions and Strategic Exploration. *Neuron, 80*(1), 223-234.

Fischer, B, & Boch, R. (1983). Saccadic eye movements after extremely short reaction times in the monkey. *Brain research, 260*(1), 21-26.

Fischer, B, Boch, R, & Ramsperger, E. (1984). Express-saccades of the monkey: effect of daily training on probability of occurrence and reaction time. *Experimental Brain Research, 55*(2), 232-242.

Gerstner, Wulfram, Kreiter, Andreas K, Markram, Henry, & Herz, Andreas VM. (1997). Neural codes: firing rates and beyond. *Proceedings of the National Academy of Sciences, 94*(24), 12740-12741.

Guo, Kun, Meints, Kerstin, Hall, Charlotte, Hall, Sophie, & Mills, Daniel. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal cognition, 12*(3), 409-418.

LaBerge, David. (1962). A recruitment theory of simple behavior. *Psychometrika, 27*(4), 375-396.

LaBerge, David. (1994). Quantitative models of attention and response processes in shape identification tasks. *Journal of Mathematical Psychology, 38*(2), 198-243.

Lee, J., Kim, H.G.R., & Lee, C. (2010). Trial-to-trial variability of spike response of V1 and saccadic response time. *J Neurophysiol, 104*(5), 2556.

Link, SW, & Heath, RA. (1975). A sequential theory of psychological discrimination. *Psychometrika, 40*(1), 77-105.

Mertens, I, Siegmund, H, & Grüsser, O-J. (1993). Gaze motor asymmetries in the perception of faces during a memory task. *Neuropsychologia, 31*(9), 989-998.

Munoz, Douglas P, & Wurtz, Robert H. (1992). Role of the rostral superior colliculus in active visual fixation and execution of express saccades. *Journal of Neurophysiology, 67*(4), 1000-1002.

Priori, A, Bertolasi, L, Rothwell, JC, Day, BL, & Marsden, CD. (1993). Some saccadic eye movements can be delayed by transcranial magnetic stimulation of the cerebral cortex in man. *Brain, 116*(2), 355-367.

Purcell, B. A., Schall, J. D., Logan, G. D., & Palmeri, T. J. (2012). From salience to saccades: multiple-alternative gated stochastic accumulator model of visual search. *J Neurosci, 32*(10), 3433-3446. doi: 10.1523/JNEUROSCI.4622-11.2012

Ratcliff, R., Hasegawa, Y.T., Hasegawa, R.P., Smith, P.L., & Segraves, M.A. (2007). Dual diffusion model for single-cell recording data from the superior colliculus in a brightness-discrimination task. *J Neurophysiol, 97*(2), 1756-1774.

Ratcliff, Roger. (1978). A theory of memory retrieval. *Psychological review, 85*(2), 59.

Rohrer, William H, & Sparks, David L. (1993). Express saccades: the effects of spatial and temporal uncertainty. *Vision research, 33*(17), 2447-2460.

Schall, J. D., Purcell, B. A., Heitz, R. P., Logan, G. D., & Palmeri, T. J. (2011). Neural mechanisms of saccade target selection: gated accumulator model of the visual-motor cascade. *Eur J Neurosci, 33*(11), 1991-2002. doi: 10.1111/j.1460-9568.2011.07715.x

Shimojo, Shinsuke, Simion, Claudiu, Shimojo, Eiko, & Scheier, Christian. (2003). Gaze bias both reflects and influences preference. *Nature neuroscience, 6*(12), 1317-1322.

Smith, Edward E. (1968). Choice reaction time: An analysis of the major theoretical positions. *Psychological Bulletin, 69*(2), 77.

Smith, Philip L, & Vickers, Douglas. (1988). The accumulator model of two-choice discrimination. *Journal of Mathematical Psychology, 32*(2), 135-168.

Stone, Mervyn. (1960). Models for choice-reaction time. *Psychometrika, 25*(3), 251-260.

Story, Giles W, & Carpenter, RHS. (2009). Dual LATER-unit model predicts saccadic reaction time distributions in gap, step and appearance tasks. *Experimental brain research, 193*(2), 287-296.

Thorpe, Simon J. (1990). Spike arrival times: A highly efficient coding scheme for neural networks. *Parallel processing in neural systems*, 91-94.

Williams, R.H.S. Carpenter & M. L. L. (1995). Neural computation of log likelihood in control of saccadic eye movements. *Nature, 377*(7), 59-62.

국문초록

원숭이의 시간 순서 판단 과제 수행 분석

서울대학교 대학원
심리학과 생물심리전공
심진우

본 연구의 목표는 원숭이를 대상으로 하는 시간순서판단 과제를 개발하고, 이 과제를 이용하여 원숭이의 시간순서 판단의 수행을 분석하는 것이었다. 두 마리의 원숭이(*Macaca Fsacicularis*)가 연구에 참여하였다. 시간순서판단 과제는 가보(Gabor) 자극을 사용하여 이중강제선택(2-Alternative-Forced-Choice) 과제의 형태로 개발하였으며 해당 과제 수행 중 동물의 반응 시간, 정답률, 반응 편향, 그리고 보상 내역을 분석하였다. 그 결과, 첫째, 정답 시행들과 오답 시행들의 평균 반응 시간은 통계적으로 유의미한 차이가 있었으나 세부 조건에 따른 차이의 패턴이 동물에 따라 달라짐을 확인하였다. 둘째, 반응 편향과 정답률 간에 유의미한 상관이 존재함을 확인하였지만 그 패턴과 상관계수의 크기는 동물간에 차이가 있었다. 셋째, 자극간 시간차가 주어진 조건에서 계산된 주관적 평가점(Point of Subjective Equality)의 편

향과, 시간차가 주어지지 않은 조건에서 계산된 반응 편향 사이에 강한 상관이 있음을 확인하였다. 넷째로 동시에 제시된 자극에 대한 피험자의 반응을 예측하기 위해, 이전 시행에서 발생한 보상 내역과 선택 내역을 이용한 로지스틱회귀 모형을 적용하였는데, 추정된 모형의 회귀 계수 값은 동물에 따라 상이하였다. 위와 같은 결과들은 동일한 조건에서 시간순서판단 과제를 수행함에도 불구하고 피험자에 따라 상이한 과제 수행 전략을 사용할 수도 있음을 시사한다.

주요어: 시간순서판단, 보상 내역, 반응 편향, 반응 시간, 원숭이
학번: 2011-20125